MORPHOLOGICAL PARAMETERS FOR MAMMAL LOCOMOTION IN SNOW[1/]

by

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Introduction

Recently, in North America, there has been increasing interest in the role of snow as a factor in the ecology of mammals. The influence of snow on ungulates and larger carnivores in the USSR was reported by Nasimovich (1955), and on ungulates in North America by Pruitt (1959), Des Meules (1964), Gilbert et al. (1970), Telfer (1970) and Kelsall and Prescott (1971).

External morphology and behavior embrace most of the many aspects of mammalian adaptation to snow. Differences in the ability of mammals to survive in snow have been observed between species and between sex and age classes within species. Since we believe that many of these differences are explicable in simple morphological terms (Kelsall, 1969; Kelsall and Telfer, 1971), we are examining such structural parameters as chest heights, which indicate the ability of mammals to cope with snow of various depths, and foot loads which indicate the ability to cope with snow of various densities and hardnesses. We have also measured hoof loads but shall not present that data here.

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Material and Methods

Field collections, reduction slaughters, roadside kills and live-trapping programs provided us with 3 coyotes (Canis latrans), 8 wolves (Canis lupus), 1 wolverine (Gulo luscus), 160 elk (Cervus canadensis), 50 white-tailed deer (Odocoileus virginianus), 117 moose (Alces alces), 5 woodland caribou (Rangifer tarandus), 24 bison (Bison bison), 20 bighorn sheep (Ovis canadensis) and 16 Dall sheep (Ovis dalli). The ungulates came from Elk Island, Jasper and Waterton Lakes national parks and from the Richardson Mountains in the Northwest Territories. The carnivores came from Jasper, north-central Saskatchewan and the Northwest Territories.

We obtained carcass weights and most chest heights from dead animals, and some chest heights from live bighorn sheep. (Chest height is the distance, with the leg extended, from the distal tip of the front hoof to the mid-line on the brisket.) Most ages were determined in the laboratory by standard procedures. We collected four feet from all specimens, but the caribou, for laboratory measurement of foot areas. We received one fore and one hind foot of each caribou and estimated the total foot areas by doubling the total measurements of both feet.

Figure 1 shows our method for measuring foot length. Figure 2 shows our technique for calculating foot and hoof area. To obtain a hoof print, we inked each foot on a large stamp pad, stamped the impression on a sheet of paper, outlined the outer ink marks by pencil and enclosed the back of the hoof by joining the posterior tips of the toe imprints (Fig. 2). The areas of the front and back parts of the

Materials and Methods

Field collections, predator control, roadside kills and live-trapping programs provided us with 5 coyotes (Canis latrans), 7 wolves (Canis lupus), 1 wolverine (Gulo luscus), 150 elk (Cervus canadensis), 30 white-tailed deer (Odocoileus virginianus), 115 moose (Alces alces), 5 woodland caribou (Rangifer tarandus), 24 bison (Bison bison), 20 bighorn sheep (Ovis canadensis) and 16 Dall sheep (Ovis dalli). The ungulates came from Elk Island, Jasper and Waterton Lakes national parks and from the Richardson Mountains in the Northwest Territories. The carnivores came from Jasper, north-central Saskatchewan and the Northwest Territories.

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Figure 1 shows our method for measuring foot length. Figure 2 shows our technique for calculating foot area. To obtain a foot print, we pressed each foot on a large stamp pad, stamped the impression on a sheet of paper, outlined the outer ink marks by pencil and enclosed the back of the foot by joining the posterior tips of the two digits (Fig. 2). The areas of the front and back parts of the

hoof impressions were measured with a planimeter. Foot load was calculated by dividing the animal's live weight, in grams (g), by the total area of its four feet in square centimeters (cm^2).

Twenty-six staff members, using the same set of hoofs, tested the precision of our methods. They measured foot lengths of a bison, a moose, an elk and a white-tailed deer, then stamped and outlined a hoof from each. Areas calculated from these measurements were within two to five percent of the mean, 95 percent of the time.

The specimens varied greatly by species, age and sex, so for each species we have grouped data for males and females 2.5 years old and up for use in illustration here. But data for carnivores, Dall sheep and caribou may have included some 1.5 year old animals. Standard errors of the mean were calculated for samples of more than nine, the mean and range only for other samples.

Results

Figure 3 catalogues chest heights, and Figure 4 foot loads for the various species by sex. In most cases where statistically adequate, comparative data were available, the mean chest heights and foot loads of males were significantly ($P > 0.05$) greater than those of females, although ranges always overlapped. This sexual dimorphism was greater in elk and deer than it was in moose. Bighorn and Dall sheep may have been exceptions to it in regard to both measurements. Smaller foot loads of female ungulates compensated for their lower chest heights. Male and female wolves had similar foot loads but differing chest heights because the males were much larger. Dall and bighorn sheep

were the only ungulates with legs shorter than those of some wolves (Fig. 3). The sheep's lower chest heights and greater foot loads account for their need for escape terrain where the wolves cannot follow them. In deep (60 cm or more) soft snow, bison, deer, caribou, elk and moose have the advantage of greater chest height over the predators. Incidentally, our observations and those of the Russians (Nasimovich, 1955) suggest that all mammals are in trouble when deep, soft snow exceeds about two-thirds of their chest height.

Foot loads (Fig. 3) tell a different story. Where snow is dense or hard enough to provide support, the three predators have a great advantage over all the ungulates except caribou. Caribou are highly adapted to snow; their mean foot load (140 g/cm^2) is only 30 to 40 g/cm^2 higher than that of wolves. Sheep, having foot loads of 300 to 400 g/cm^2, are surprisingly light on their feet. Deer have a significant advantage over moose and elk. Bison have relatively short legs and their foot loads range from 760 to 1,060 g/cm^2; in comparison to other species, they are poorly adapted to snow.

Discussion

Animals with higher chest heights can cope with soft, deep snow. Conversely, species with large foot loads are at a disadvantage in dense or crusted snow, where they sink deeply. The survival value of the morphological parameters considered in this study depends on the frequency and duration of various types of snow cover. We have not yet explored the zoogeographical aspects of our study, but Russian studies suggest that there are many (Nasimovich, 1955; Formozov, 1946).

In soft snow, predators cannot move about as freely as ungulates, although wolves may have an advantage over sheep. On hard snow, generally in late winter, predators are more mobile than ungulates, although wolves are only marginally more so than caribou. As a logical extension of our present work the mammals investigated should now be studied in various types of snow.

Acknowledgements

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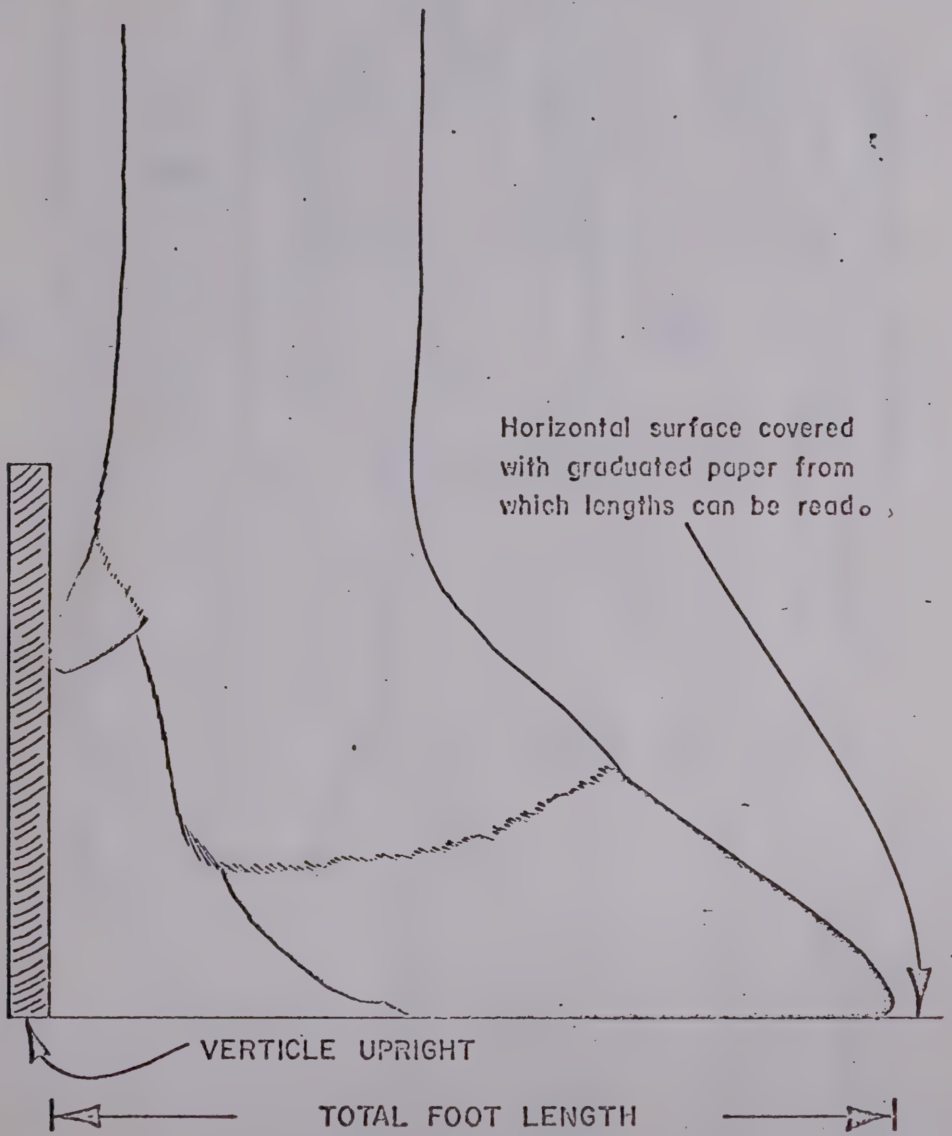

Figure 1- A method for measuring total foot length of ungulates.

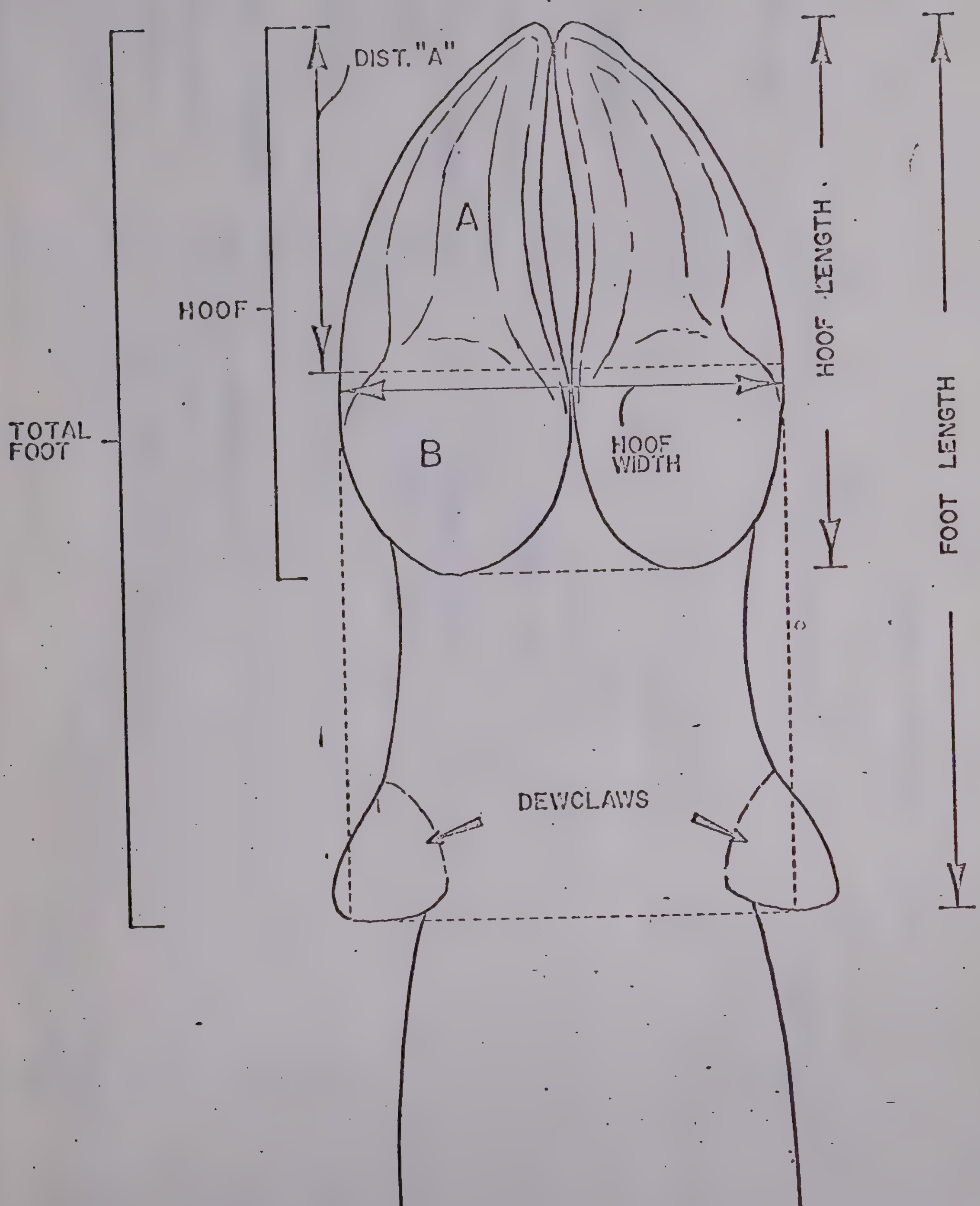

Figure 2 - A diagram of an ungulate foot showing foot and hoof lengths and hoof outline. Total foot area is obtained by adding the area of the front part of the hoof (A) to the area of the rectangle (foot length minus distance "A" times hoof width).

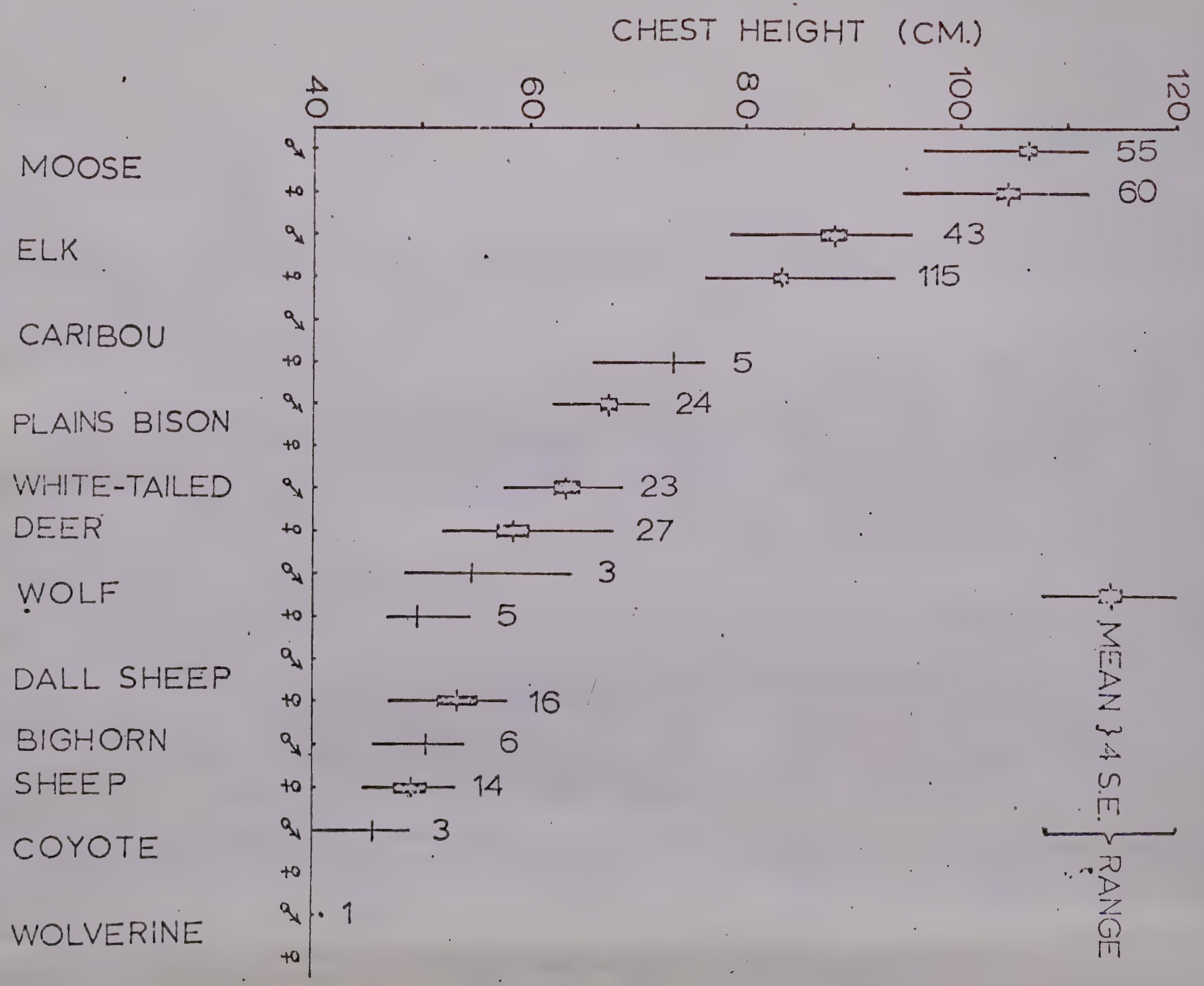

Figure 3. Chest heights for 7 ungulates and 3 predators from western Canada

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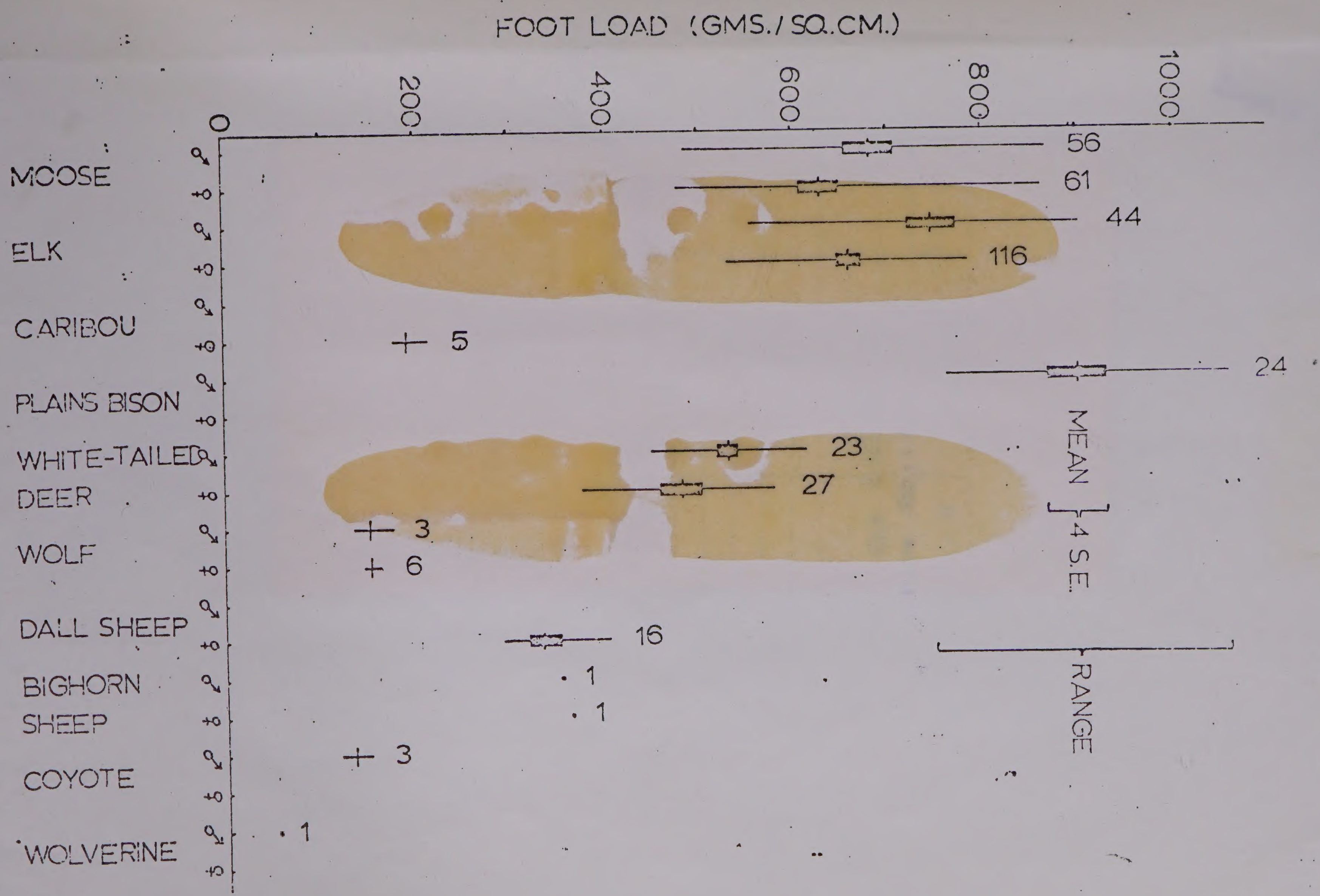

Figure 4. Foot loads for 7 ungulates and 3 predators from western Canada